

**REVIEW AND  
SYNTHESIS****The need for integrative approaches to understand and conserve migratory ungulates**

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**Abstract**

Over the last two centuries overhunting, anthropogenic barriers and habitat loss have disrupted many ungulate migrations. We review the literature on ungulate migration disruptions and find that for many species the disruption of migratory routes causes a rapid population collapse. Previous research has focused on the proximal ecological factors that might favour migration, particularly spatiotemporal variation in resources and predation. However, this does not provide an adequate basis for understanding and mitigating anthropogenic effects on migratory populations. Migration is a complex behaviour and we advocate an integrative approach that incorporates population dynamics, evolution, genetics, behaviour and physiology, and that borrows insights and approaches from research on other taxa. We draw upon research on avian migration to illustrate research approaches that might also be fruitful in ungulates. In particular, we suggest that the migratory cycle should be evaluated in the context of seasonal population limitation, an approach we highlight with a preliminary demographic perturbation analysis of the Serengeti wildebeest (*Connochaetes taurinus*) population. We provide suggestions for avenues of future research and highlight areas where we believe rapid progress can be made by applying recent advances in theory, technology and analytical approaches.

**Keywords**

Habitat barriers, habitat loss, life-history tradeoffs, migratory cycle, overhunting, population limitation, sensitivity analysis, site fidelity, Tarangire ecosystem.

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**INTRODUCTION**

Animal migrations are among the most spectacular of natural phenomena, capturing the imagination of both scientists and the public due to the sheer numbers and relentless movements of thousands of individuals over large spatial scales. Among the most awe-inspiring are ungulate migrations. The paucity of intact ungulate migrations today (Berger 2004) underscores the need for effective conservation. Yet, our understanding of the biology of ungulate migration is fragmentary. We do not know the connection between migration and population limitation for nearly any ungulate migration, nor do we understand the life-history trade-offs that have led to the evolution of migration. The fact that ungulate grazing can have important ecosystem impacts (McNaughton & Georgiadis 1986; Collins *et al.* 1998) lends further urgency to efforts to understand their evolution, behaviour and demography.

In this review, we focus on several aspects of the biology and conservation of migratory ungulates that are crucial yet understudied. First, we examine the population consequences of recent disruptions of ungulate migrations. Secondly, we focus on the features of ungulate life histories that shape their population dynamics and migratory behaviour. Thirdly, we examine the demographic tradeoffs involved in migratory life histories and use demographic perturbation analysis to suggest an approach to understanding the costs and benefits of migration. Next, we discuss the behaviours that underlie migration, with an emphasis on flexibility in the face of anthropogenic disturbances. We end with a discussion of what is needed next in migration research and how best to use improved understanding to better conserve ungulate migrations. Our overall goal is to promote an integrated understanding of forces that drive migrations and the consequences of their disruption.

## Disruption of ungulate migrations

Over the last two centuries, ungulate migrations have been severely disrupted by human activities. The historical accounts of the precipitous decline of the springbok [*Antelope marsupialis*; taxonomy throughout follows Wilson & Reeder (2005)] migration or trek in Southern Africa, which exceeded tens of thousands of animals at its height (Skinner 1993), and the American bison (*Bison bison*) in the Great Plains of North America which numbered as many as 30 million animals (Lott 2002) as well as recent sudden declines of ungulate migrations discussed below highlight the extreme vulnerability of the remaining ungulate migrations to human disturbance.

Three human activities that have contributed to the decline of ungulate migrations are overhunting, anthropogenic barriers and habitat loss (Table 1). Possibly the best known example of overhunting leading to the collapse of a migration and species is the American bison. Beginning in the early 1800s and extending through the late 1870s, market hunters in the Great Plains of North America harvested up to 5 million animals annually (Trefethen 1975). By the early 1880s, the American bison was extinct throughout its entire range with the exception of small populations in Yellowstone and Wood Buffalo National Parks and a semi-domesticated herd in Texas (Trefethen 1975; Dary 1989; Foster *et al.* 1992). More recently, overhunting in Inner Mongolia, China, Kalmykia, Russian Federation and Kazakhstan has led to the drastic decline in the migration patterns and abundance of several ungulate species (Wang *et al.* 1997; Milner-Gulland *et al.* 2001). Wang *et al.* (1997) reported that between the mid-1950s and the early 1990s the geographic distribution of the Mongolian gazelle (*Procapra gutturosa*) in Inner Mongolia, China declined by 75% as a result of overhunting. They estimate, based upon harvest records and interviews with local leaders, that in the late 1950s upwards of one-quarter of the estimated population of 2 million was harvested annually while between 1987 and 1989 the annual harvest was one-third of the estimated population of 500 000. In Kazakhstan and Kalmykia, Russian Federation saiga (*Saiga tatarica*) populations declined by 35–56% annually between 1998 and 2000 as a result of poaching (Milner-Gulland *et al.* 2001). The predictability of migration routes and timing, as well as the density of animals have almost certainly contributed to the overhunting of some ungulate species.

Anthropogenic barriers in the landscape (e.g. fences, roads, railroads, pipelines, reservoirs) have also disrupted many ungulate migrations. In Southern Africa, many rangelands, transnational boundaries, and protected areas have been fenced to prevent the transmission of disease among livestock and wildlife as well as to provide protection against poaching. This fencing has severely

disrupted many ungulate migrations and has resulted in a dramatic decline in the abundance of several migratory species (Williamson & Williamson 1985; Whyte & Joubert 1988; Spinage 1992; Ben-Shahar 1993; Berry 1997). In Central Asia, railroads have created barriers to ungulate migrations. In Mongolia, the Ulaanbaatar–Beijing railroad is believed to be the most important causal factor in closing the historic east–west migration of Mongolian gazelle (Lhagvasuren & Milner-Gulland 1997; Ito *et al.* 2005).

Habitat loss, primarily due to agricultural expansion, has also disrupted many migratory ungulate populations. Researchers working in the Masai Mara ecosystem in southern Kenya reported a decline of 81% between the late 1970s and 1990s in the migratory wildebeest (*Connochaetes taurinus*) population (Ottichilo *et al.* 2001). Based upon a comparison of land use and human activities in the Masai Mara with that on the Tanzanian side of the Serengeti-Mara region, where wildebeest populations have remained stable, they attribute this decline to large-scale agricultural development (Homewood *et al.* 2001; Serneels & Lambin 2001). Similarly, migratory wildebeest in the Tarangire ecosystem in northern Tanzania have declined by 88% over 13 years (Tanzania Wildlife Research Institute 2001) due largely to agricultural development adjacent to the park (see Box 1).

On inspection of Table 1, two important features stand out. First, migratory ungulate species appear to vary in their sensitivity to human disturbance. In Southern and East Africa, wildebeest, hartebeest (*Alcelaphus buselaphus*), and zebra (*Equus burchellii*) populations are particularly sensitive to the disruption of migratory routes and have frequently declined in protected area ecosystems. Secondly, for sensitive species the population response to migration disruption is often sudden and severe. In East and Southern Africa wildebeest and hartebeest populations have declined by 70–95% over time periods of 8–20 years following the disruption of migratory routes (Table 1). The reasons for varying sensitivity and rapidity of population crash are the focus of the following three sections.

## Migration in the context of population limitation

Our understanding of why many migratory ungulate species decline so suddenly in response to human activities is poor. One reason for this is that we have little understanding of how different phases of the migratory cycle fit into the processes of population limitation. For a few migratory bird species our understanding of migration has been advanced by considering changes occurring in both breeding and non-breeding season habitat in the context of the overall limitation of the population (Sherry & Holmes 1996; Runge

**Table 1** Population response of migratory ungulate species to human activities in Africa, Asia and North America

Location	Species	Human activities	Population response	Reference
Lake Nakuru NP, Kenya	Hartebeest <i>Alcelaphus buselaphus</i> Giraffe <i>Giraffa camelopardalis</i>	Fencing	Local extinction	Mwangi 1998
Lake Manyara NP, Tanzania	Hartebeest	Agricultural expansion	Local extinction	Newmark 1996
Tarangire NP and ecosystem, Tanzania	Wildebeest	Agricultural expansion and overhunting	Substantial decline (88, 90 and 95%, respectively, 1998–2001)	Tanzania Wildlife Research Institute 2001
Kruger NP, South Africa	Hartebeest <i>Oryx</i> <i>Oryx gazelle</i> Wildebeest	Fencing	Substantial decline (87% in one sub-population, 1965–1979)	Whyte & Joubert 1988
Northern Kalahari, Botswana	Zebra <i>Equus burchelli</i>	Fencing	Local extinction	Williamson & Williamson 1985
Etosha NP, Namibia	Wildebeest	Fencing	Substantial decline (85%, 1955–1973)	Berry 1997
Southern Kalahari, Botswana	Wildebeest Hartebeest	Fencing	Substantial decline (90% and 70%, 1979–1987; 1981/1987*–1986/1990 respectively)	Spinage 1992
Sabi-Sand Wildtuin Game Reserve, South Africa	Wildebeest	Fencing	Substantial decline (c. 66% and c. 33%, 1963–1977)	Ben-Shahar 1993
Masai Mara ecosystem, Kenya	Zebra Wildebeest	Agricultural expansion	Substantial decline (81%, 1977–1997)	Homewood <i>et al.</i> 2001; Serneels & Lambin 2001; Ottichilo <i>et al.</i> 2001
South Africa, Botswana, Namibia	Springbok <i>Antidorcas marsupialis</i> Wildebeest	Disease and overhunting	Substantial decline	Skinner 1993
Northern Botswana and Namibia	Wildebeest	Fencing	Substantial decline (c. 92% over unspecified period)	Estes 1969
Kalmykia, Russian Federation	Saiga antelope <i>Saiga tatarica</i>	Overhunting	Substantial decline (93%, 1980–2000)	Milner-Gulland <i>et al.</i> 2001
Kazakhstan	Saiga antelope	Overhunting	Substantial decline (78%, 1980/1990–2000)	Milner-Gulland <i>et al.</i> 2001
Inner Mongolia, China	Mongolian gazelle <i>Procapra gutturosa</i>	Overhunting	Substantial decline in geographic range (c. 75%, 1950s/1970s–1994/1995)	Wang <i>et al.</i> 1997
Western Mongolia	Mongolian gazelle	Railroad construction, overhunting, human settlement	Substantial decline since the 1950s	Lhagvasuren & Milner-Gulland 1997
Great Plains, Canada and United States	American bison <i>Bison bison</i>	Overhunting	Local extinction throughout its historic range	Trefethen 1975
Central California, United States	Mule deer <i>Odocoileus hemionus</i>	Human settlement, reservoir & road construction	Substantial decline (c. 80%, 1952–1977)	Bertram & Rempel 1977
Northern California, United States	Mule deer	Reservoir construction	Decline (1960–1963)	Kie <i>et al.</i> 1982; Loft <i>et al.</i> 1984
Newfoundland, Canada	Caribou <i>Rangifer tarandus</i>	Reservoir construction	Minimal impact	Mahoney & Schaefer 2002
Prudhoe Bay, Alaska, United States	Caribou	Road construction	Displacement and increased density in non-roaded areas	Nellemann & Cameron 1998

\* - dates separated by a “\” indicate that in the original citation a single value was presented to represent population size over a period of years.

**Box 1** The Tarangire migration

East Africa's large mammal migrations are among the most spectacular and well known of all large mammal migrations, worldwide. One of the few remaining sites in Africa where a significant seasonal migration still occurs is in the Tarangire ecosystem. Tarangire National Park lies in the Maasai Steppe in northern Tanzania and was established in 1961 in large part to serve as a dry season refuge for migratory species (Lamprey 1963, 1964). Here, large populations of wildebeest, zebra, and Grant's gazelle (*Gazella granti*) and smaller populations of hartebeest, eland (*Taurotragus oryx*), oryx (*Oryx gazella*), Thomson's gazelle (*Gazella thomsoni*), buffalo (*Syncerus caffer*), and giraffe (*Giraffa camelopardalis*) migrate 10–110 km out of the park at the beginning of the rainy season in late November and back into the reserve at the beginning of the dry season in early June (Lamprey 1963, 1964; Kahurananga & Silkiluwasha 1997; Tarangire Conservation Project (TCP) 1998).

Historically, migrations occurred in a north-easterly, northerly, easterly, south-easterly and south-westerly direction (Lamprey 1963; Fig. 1). Yet, because of increasing human activities adjacent to the park, particularly agricultural development, migratory routes are now restricted primarily to the east and southeast of the park (Borner 1985; TCP 1998) (Fig. 1). Since the 1940s, human population and agricultural cultivation have increased four to sixfold in the Tarangire ecosystem (Yanda & Mohamed 1990; Mwalyosi 1991; Gamassa 1995). As of the early 1990s, approximately 10.5% of lands in the Tarangire ecosystem were under agricultural cultivation, with much of this agricultural expansion abutting the park (Mwalyosi 1991). Since the early 1990s the agricultural development adjacent to the park has accelerated. In addition, sport and illegal market hunting occurs on lands adjacent to the park.

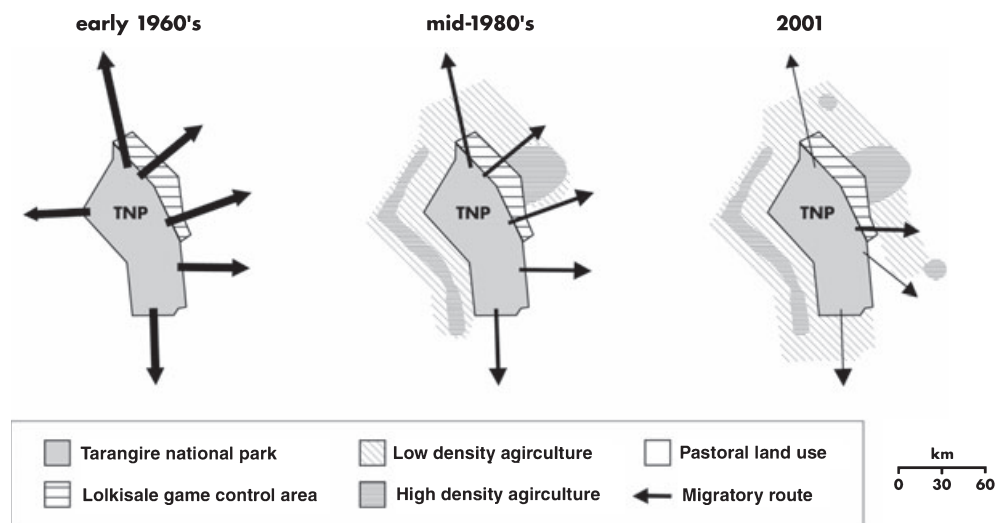
As traditional migratory routes have been disrupted, many ungulate populations have declined. Between 1988 and 2001, wildebeest, hartebeest and oryx populations declined within the Tarangire ecosystem by 88, 90 and 95% respectively (Tanzania Wildlife Research Institute 2001). In contrast, populations of zebra, giraffe, buffalo and Grant's gazelle during this same period have remained relatively stable or declined only slightly (Fig. 2). A comparison of the inter-specific demographic responses of migratory species in the Tarangire ecosystem to the disruption of traditional migratory routes should offer valuable insights into the costs and benefits of ungulate migrations and to the reasons for variable inter-specific sensitivity.

& Marra 2005; Holmes 2007). In large part, this work has been inspired by concern over population declines in migratory birds, with neotropical species breeding in North America receiving much of the attention (e.g. Stotz *et al.* 1996). When a migratory population declines, its reliance on at least two different locations begs the question: in which habitat are the changes occurring that are driving the decline? While useful, this simplistic dichotomy obscures the complex ways in which seasons are likely to interact in limiting populations. Sutherland (1996) showed it is impossible to predict the effect of habitat loss in one part of the migratory cycle without knowledge of demographic rates and their density-dependence in other parts of the cycle. A reduction of habitat in one season can be partially compensated by density-dependent responses in the other season. Nonetheless, the general conclusion is that habitat loss in the season with more stringent density-dependence has the greatest effect (Sutherland 1996). Thus, population limitation over the entire migratory cycle must be considered when gauging the effects of changes within any one habitat.

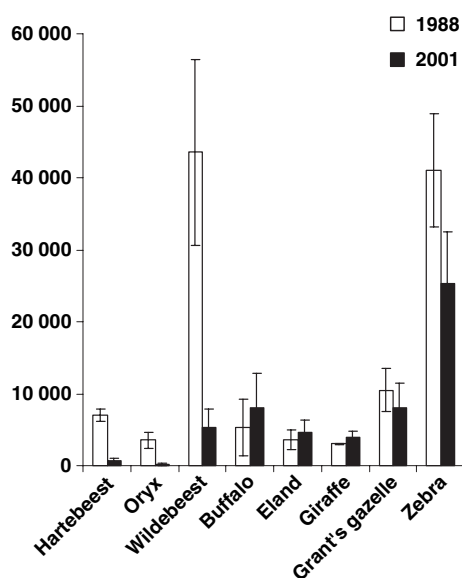
In migratory birds, physiological linkages between habitats have also been demonstrated in what have been termed 'seasonal carryover effects' (Marra *et al.* 1998; Norris *et al.* 2004). Environmental conditions in one place or season can

create subtle differences among individuals or populations that affect demographic rates in the subsequent season. The carry-over may be at the population level in terms of population size coming out of a particular season or at the individual level in the form of heterogeneity in condition due to different experiences in the preceding season (Runge & Marra 2005). For instance Marra *et al.* (1998) demonstrated that the quality of winter habitat occupied by individual male redstarts (*Setophaga ruticilla*) was correlated with arrival date and arrival condition at the spring breeding habitat. Both of these measures are tightly linked to male reproductive success in many passerine migrants. Indeed, in a subsequent study winter habitat quality was shown to affect the number of young fledged in both male and female redstarts (Norris *et al.* 2004). Thus, the effects of anthropogenic changes in one seasonal habitat might only be expressed in another season and habitat. While these seasonal interactions operate similarly to seasonal time-lags or cohort effects in non-migratory populations, in a migratory context they have the important distinction of occurring in spatially distinct habitats.

Ungulates are amenable to the study of carry-over effects, as, in principle, individuals can be followed through all phases of the migratory cycle. Few studies of large migratory mammals, however, have attempted to account for interac-



**Figure 1** Changes in ungulate migration routes between the early 1960s and 2001 in the Tarangire ecosystem in north-central Tanzania. Thickness of arrows represents approximate relative numbers of animals using these migratory routes in and out of the park.



**Figure 2** Change in population size ( $\pm 1SE$ ) of migratory ungulate species in the Tarangire ecosystem between 1988 and 2001 (data from Tanzania Wildlife Research Institute 2001).

tions between different seasons. In greater kudu (*Tragelaphus strepsiceros*), Owen-Smith (1990) showed that seasonal juvenile and yearling survival is strongly related to the ratio of rainfall in the previous season to current population biomass. However, whether subtle individual differences in body condition or migration timing entering each season – a function of conditions during the previous season(s) – influence survival or reproduction, is largely unknown for migratory species. Among non-migratory ungulates, captive

elk show delayed reproduction in the spring and a lower probability of survival of calves in the winter when fed low quality forage in the late summer and fall (Cook *et al.* 2004). In roe deer (*Capreolus capreolus*), the quality of spatially varying resources in the springtime strongly influences the body mass of individuals during the winter (Pettorelli *et al.* 2003).

The phase of the ungulate migratory cycle that has received perhaps the least attention is the actual movement period. Researchers have paid little attention to the demography of migratory populations *while on migration*, largely due to the difficulty of tracking individuals during this period. Energetic and mortality costs and density dependence during migration are likely to have important effects on population dynamics. There may be more scope for density-dependence during migration in mammals than in birds; long distance migratory mammals such as caribou (*Rangifer tarandus*) in Alaska and northern Canada, and wildebeest and zebra in the Serengeti generally spend more time on migration and are less able to move across large areas without suitable resources. Positive density-dependence is likely in some situations, especially as driven by local predator saturation. Negative density-dependence might occur because local food competition and the per capita probability of trampling or drowning should be reduced in sparser herds (Sinclair 1983).

Seasonal comparisons of mortality data for wildebeest in Serengeti and Ngorongoro Crater do suggest that migration has a significant cost. During a period of population growth, the Serengeti wildebeest experienced 3% annual mortality because of the migration, either through drowning, injury, or the indirect effects of energy expenditure and 7%

mortality during the non-migratory period (Sinclair 1983). This demonstrates the relatively high cost of migration (30% of total mortality). Similarly, Hebblewhite and Merrill (2007) found predation risk in migratory elk (*Cervus elaphus*) to be highest during migration.

Particularly useful in untangling these seasonal effects would be demographic studies and population models of migratory ungulates that separate the year into breeding, non-breeding and migratory periods and account for fecundity and survival in each of those periods (e.g. Sillett & Holmes 2002; Runge & Marra 2005). This would facilitate the quantification of the costs and benefits of migration addressed below. These kinds of studies would require marking or recognition of large numbers of individuals (see below).

To understand migration, in the context of population limitation, it is necessary to understand ungulate demography and life history and how these interact with potential limiting factors in the various migratory habitats. Below we highlight those aspects of ungulate life history that are particularly salient to an understanding of migration. This review is somewhat complicated by the fact that many of the most detailed demographic studies of ungulates have been done on resident temperate populations in the absence of large predators [e.g. red deer, soay sheep (*Ovis aries*)]. However, as the limiting factors and density dependence in non-migratory ungulates do not appear broadly different from those of migratory ungulates, we still consider these studies.

1. *Juvenile survival and age at first reproduction are often the demographic parameters most sensitive to environmental variation and density-dependence.* In general, density and weather tend to first affect juvenile survival, then reproductive rates of young females [this order may be reversed for species greater than 50 kg (Gaillard *et al.* 2000)]. Only at high densities, in the face of severe weather, is there an effect on the fecundity of prime-age adults. Adult survival is affected only under the most severe conditions (Gaillard *et al.* 2000; Eberhardt 2002).

2. *Adult survival often has the highest population growth elasticity, but also shows the lowest variation* (Gaillard *et al.* 2000; Heppell *et al.* 2000). As in many moderate- to long-lived animals, population growth rates are highly sensitive to ungulate adult survival; however, these survival values usually exhibit only small amounts of natural variation. [Sensitivity is the change in population growth rate caused by a unit change in a particular demographic rate; elasticities are standardized sensitivities that allow for direct comparison among rates (Caswell 2001)]. Thus, under usual patterns of environmental variation, juvenile survival will often drive variation in population growth rate (Gaillard *et al.* 2000). At high density adult survival has sometimes been shown to drive variation in population growth rates (Albon *et al.* 2000). If some perturbation can cause significant variation in adult survival, it can have large effects on population growth rate. Thus poaching, in which adults are usually targeted, and to which

migratory ungulates are generally more vulnerable than residents, has the potential to have large effects on population growth rates.

3. *Limitation results from the interaction of density-dependent and density-independent processes* (Saether 1997), with food the most common limiting resource. Density-dependence interacts strongly with environmental variability; it is only expressed under certain climatic conditions. Evidence for resource limitation among non-migratory ungulate populations, often in the absence of predators, has emerged from several seminal long-term studies: red deer (*Cervus elaphus*) on the Isle of Rhum (Bobek 1977; Clutton-Brock *et al.* 1985; Albon *et al.* 2000), Soay sheep on the Island of Hirta (Grenfell *et al.* 1992; Milner *et al.* 1999), bighorn sheep (*Ovis canadensis*) in Canada (Festa-Bianchet *et al.* 1998), reindeer (Skogland 1985) and roe deer in Europe (Gaillard *et al.* 1993; Toigo *et al.* 2006). However, density-dependence is strongly expressed only during periods of harsh weather (Coulson *et al.* 2001; Stenseth *et al.* 2004).

Long-term studies in Africa suggest that many savannah grazers are resource-limited during the dry season (July–December) [white-eared kob (*Kobus kob*): Fryxell 1987; greater kudu: Owen-Smith 1990; wildebeest: Sinclair *et al.* 1985; Sinclair & Arcese 1995; Mduma *et al.* 1999]. Many of these studies quantify food availability indirectly, using a highly significant relationship between seasonal or annual rainfall accumulation and the rate of plant growth (e.g. Mduma *et al.* 1999). An analysis of the long-term demographic records from Kruger National Park, South Africa found strong relationships between juvenile survival and the amount of rainfall during the previous dry season in seven out of eight ungulate species (Owen-Smith *et al.* 2005). Thus, in systems with and without predators, food has been shown to be an important limiting resource.

Overall, the strong interaction of negative density-dependence with climate suggests that long-term data will be needed to carefully assess population dynamics created by density-dependence for any migratory ungulate. This need for long data sets is also emphasized by the evidence that at least some ungulates have non-linear density-dependence with strongly overcompensating responses near carrying capacity (Fowler 1987; McCullough 1997; but see Owen-Smith 2006). If habitat loss occurs in a population near carrying capacity, the density-dependent response in population growth rate could be rapid and severe. This suggests one hypothesis for the apparent severity of the collapse of many migratory populations.

4. *In tropical migratory ungulates clear evidence of predator limitation is less common. In cases where predation is important it usually interacts with resource availability.* Predators, parasites and hunting can also explain variation in vital rates of wild ungulates, and may interact with resource availability in important ways (Skogland 1991). Evidence for limitation by

predation is more common in north temperate ungulates, particularly by wolves (*Canis lupus*; Bergerud *et al.* 1983; Bergerud & Elliott 1998; Vucetich *et al.* 2005; Andersen *et al.* 2006). Disease [waterbuck (*Kobus ellipsiprymnus*): Melton 1987] and hunting (buffalo: Sinclair 1977) have also been demonstrated to limit non-migratory populations.

These factors may often interact with food availability; malnourished individuals have greater susceptibility to predators or parasites. Likewise, predation risk affects food availability. Animals may alter foraging behaviour to reduce predation risk, thereby reducing feeding rates or access to high quality forage (Sinclair & Arcese 1995). Predation limitation may also be more common in smaller-bodied ungulates (Sinclair *et al.* 2003), however, migration is also less common in smaller species.

Plains zebra are a notable exception to the pattern of food limitation among tropical migratory ungulates, as predation explains more variation in survival than resources or rainfall (Mills & Shenk 1992; Grange *et al.* 2004; Owen-Smith *et al.* 2005). There appears to be an interaction between predation and food availability; predation is particularly important during the dry season when zebra forage in areas of greater predation risk (Hopcraft *et al.* 2005). There are also important interactions of predation with other resources. During the dry season in seasonally arid systems, water-dependent wildlife and livestock must congregate near water points on a regular basis (Western 1975; Illius & O'Connor 2000) creating local food competition (Andrews 1988) and attracting high densities of predators (Spong 2002; Hopcraft *et al.* 2005).

5. *Importance of interactions.* The preceding points all highlight the importance of interactive processes in ungulate population dynamics. Important interactions include: food and water, density and climate, predation and resource availability. The strong influence of these interactive factors suggests that single-factor explanations for changes in migratory populations are unlikely to be satisfactory.

### Benefits and costs of ungulate migration

As reviewed above migratory ungulates share a life history that can be impacted by multiple, interacting factors. Thus, to understand migratory population dynamics and evolution, analytical techniques that synthesize these diverse influences are needed. Demographic perturbation analysis (Caswell 2001) is one technique that can be used to help evaluate the net effect of the costs and benefits of migration and provide insight into the selective forces that shaped this complex behaviour.

While it is clear that migration behaviour must have both costs and benefits for large mammals, the exact nature of this tradeoff has proven elusive. The costs are obvious enough; the direct and indirect costs of travel can be

substantial for land-bound animals including the energy expended in travel and the risks of predation or accidental injury from travelling through unknown and dangerous areas. However, even for temperate-tropical migratory birds, long-standing controversies about the benefits of migration remain. For ungulates, which rarely migrate far enough to move between major biomes, it is even less clear what the benefits of migration really are. Still, the list of possible, fundamentally different benefits of migration is fairly short:

- (1) Following seasonally changing food quantity, phenology and/or accessibility (e.g. areas with abundant food in the summer and areas with low snow cover in the winter; e.g. Maddock 1979; Mduma *et al.* 1999; Albon & Langvatn 1992; Pettorelli *et al.* 2005).
- (2) Gaining access to critically limiting resources that differ by location and season (e.g. water in the dry season and limiting nutrients in the wet season; e.g. Kreulen 1975; Murray 1995).
- (3) Seasonal escape from predators, parasites or insect harassment (e.g. Sinclair 1979; Fryxell *et al.* 1988).

Each of these possible benefits may affect multiple life-history stages or vital rates. For example, travelling to acquire critical nutrients in areas far from permanent water sources (and thus that are only accessible during the wet season) may improve reproductive success alone, or may be important for adult survival as well. Which vital rates are benefited or reduced is important, as they determine the actual fitness benefits of migration and hence the extent to which migration benefits outweigh the inevitable costs. Thus, although each benefit or cost of migration has some empirical support, little progress has been made to integrate these ideas or to rigorously test their relative importance in different circumstances.

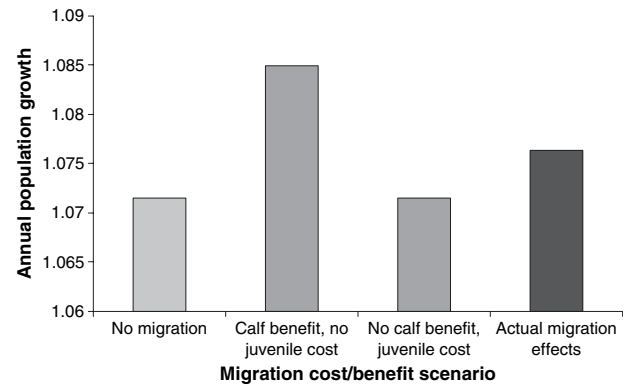
One way to make such a synthesis is to take a life history approach that permits a quantitative assessment of the magnitude of migration benefits required to outweigh the inevitable migration costs. This is made easier by the relatively similar life histories of the most highly migratory ungulates – and, indeed, this similarity itself is a clue about the structures of costs and benefits that will favour migration behaviour. As reviewed above, ungulate life histories typically have relatively high and constant adult survival, and lower and more variable calf survival. Although the elasticities of adult survival are greater than that of fecundity or calf survival, adult survival shows much lower environmental sensitivity. Because litter sizes are small and highly constrained fecundity is not an axis on which selection is likely to act very strongly. This leaves calf survival as the most likely arena in which costs and benefits of migration can act. Ungulate migrations might thus be thought of as a life-history adaptation to increase calf survival. Indeed, one line of evidence that indirectly

supports this hypothesis is that the spatial fidelity of migratory large mammals to their calving range is much higher than to other portions of their migratory range [e.g. caribou in northwest Ontario (Ferguson & Elkie 2004), mule deer (*Odocoileus hemionus*) in the southern Idaho (Brown 1992), white-tailed deer (*Odocoileus virginianus*) in the Adirondack Mountains (Aycrigg & Porter 1997) and Yellowstone National Park (Dusek *et al.* 1989), sika deer (*Cervus nippon*) in eastern Hokkaido, Japan (Sakuragi *et al.* 2004) and wildebeest in the Serengeti (Maddock 1979)].

A simple stage-structured demographic model for a migratory ungulate such as the wildebeest illustrates these ideas. We group females into first year animals (calves), second year juveniles and adults. We break annual survivorship into survival over the 6 months spent in dry season habitat, and survival over the 6 months spent in wet season habitat. This results in the following annual matrix model for a census taken immediately after birthing:

$$\begin{pmatrix} S_{c,w}S_{c,d}F_j & S_{j,w}S_{j,d}F_a & S_{a,w}S_{a,d}F_a \\ S_{c,w}S_{c,d} & 0 & 0 \\ 0 & S_{j,w}S_{j,d} & S_{a,w}S_{a,d} \end{pmatrix}. \quad (1)$$

Here, survival rates are indexed by age (c = calf, j = juvenile, a = adult) and season (d = dry and w = wet). Fecundity is distinguished for juveniles and adults ( $F_j$  vs.  $F_a$ ). To illustrate how this model might be used to understand the possible costs and benefits of migration, we used demographic data from Mduma *et al.* (1999) on Serengeti



**Figure 3** Comparing the costs and benefits of wildebeest migration for population growth rate ( $\lambda$ ). Predicted growth rates are shown for no migration scenario, only calf benefits or only juvenile costs of migration, and both costs and benefits. Results show that benefits to calves strongly outweigh estimated costs to juveniles for individual fitness and population growth. Original demographic estimates from Mduma *et al.* 1999; Vital rates used in these predictions include first year (calf), juvenile, and adult wet season (0.994, 0.726, 0.976) and dry season (0.531, 0.778, 0.965) survivals, and juvenile, and adult female fecundities (0.14–0.44). All survival and fecundities rates used are for 1994 (Mduma *et al.* 1999).

wildebeest, not nearly equalling the benefits to juveniles of migration (Fig. 3) – again assuming that wet and dry season differences are entirely due to habitat differences that arise because of migration between these areas.

$$\begin{pmatrix} (0.996)(0.531)(0.14) & (0.726)(0.778)(0.44) & (0.976)(0.965)(0.44) \\ (0.996)(0.531) & 0 & 0 \\ 0 & (0.726)(0.778) & (0.976)(0.965) \end{pmatrix}. \quad (2)$$

wildebeest. While we use the data here in a simplistic way, it will serve to illustrate the utility of this approach.

Data from 1994, a fairly typical weather year, show calf survival during the wet season of their birth as 0.996 while survival over the subsequent 6 months, during the dry season (July–December), is only 0.531 (Mduma *et al.* 1999). This model yields an annual population growth rate of  $\lambda = 1.07$ . Going a step farther, if we assume that the striking difference in wet and dry season calf survival is the result of migration to more favourable habitat alone, then the change in  $\lambda$  values for models with lowered wet season survival give an indication of the benefit of migration (Fig. 3). However, migration must also entail some cost. A possible sign of this is the lowered 6-month survival of juvenile wildebeest in wet (0.726) vs. dry (0.778) habitats. This possible increase in juvenile survival if animals were not to migrate during the wet season has a small effect on

We reiterate that the application of the data in this example requires unrealistic assumptions about the causes of differences between seasonal demographic rates. In reality, these differences are likely due to seasonal changes that are independent of migratory status such as regional-scale changes in food and nutrient availability as well as changes in foraging strategy between dry and wet seasons. With better information, such as survival rate estimates during the migratory period, real tradeoffs in survival rates with and without migration could be assessed using a demographic approach, ideally elaborated by inclusion of density dependent interactions with habitat and seasonal limitations. A particularly powerful approach would be to contrast the life history patterns for coexisting migratory and non-migratory sub-populations (e.g. Hebblewhite & Merrill 2007). With this type of information, demographic methods to compare and partition the contributions to

differences in population performance, such as life table response experiments (Caswell 2001) would be especially informative, again, most realistically so if extended to include density effects.

### Do ungulates exhibit a 'migratory syndrome'?

An important question for conservation is whether animals *are able* to respond to novel or changing landscapes within their life times, and, if so, *how quickly* those changes take place. In large measure the answer to these questions lies in the degree to which migration has a genetic basis, how responsive it is to environmental influences, and how dependent is it on individual and social group memory. Presently, our understanding of these issues in ungulates is rudimentary. However, other taxa, particularly birds and insects, are much better suited to both field and laboratory studies of behaviour, genetics, neurobiology and physiology and thus we should look to the research on those taxa for guidance.

Migration is a complex behaviour that is governed by a number of traits that have varying degrees of genetic control and context sensitivity. In insects and birds a 'migration syndrome' has been well described in a small number of species (Dingle 2006; Roff & Fairbairn 2007). This constellation of traits includes navigation, timing of migration, site fidelity, social behaviour and morphological and physiological adaptations and acclimations for migration. In a handful of species the genetic basis and genetic covariance (Fairbairn & Roff 1990; Pulido & Berthold 2003) among these traits has been determined. Knowledge of this syndrome has been very useful in understanding and predicting changes in migration due to climate change and other anthropogenic factors (Coppack & Pulido 2004; Nilsson *et al.* 2006).

In birds, migration has a substantial genetic component as revealed by studies of heritability (Pulido & Berthold 2003), common garden experiments (Helm *et al.* 2005), selection experiments (Berthold *et al.* 1992; Pulido *et al.* 1996), and field studies of selection (Brown & Brown 2000). Components of the migration syndrome with demonstrable heritability include wing morphology, and timing and amount of migratory activity (Pulido & Berthold 2003; Pulido 2007). In passerines, which are short-lived and migrate singly at night, the timing and migratory route are controlled by an inflexible genetic program in first-time migrants (Berthold 1996). On subsequent trips, migratory behaviour is more environmentally responsive. In longer-lived social birds, such as geese, swans and storks, the genetic program is less important (although still present) and social learning more important (Rees 1988; Chernetsov *et al.* 2004). These latter species are probably more appropriate analogs to migratory ungulates, which are relatively long-lived and often migrate in herds.

Bird migration appears to be an evolutionarily and ecologically labile trait. It is well distributed in avian phylogenies and often non-migratory species are the nearest relatives of migratory species (Helbig 2003). Also, many bird populations are partially migratory; a percentage of the population migrates to breed and the rest are year-round residents. Migrations have appeared in previously non-migratory populations (Able & Belthoff 1998) and have dramatically changed in locations and directions (Berthold *et al.* 1992) within a few generations in some bird populations. The percent of the population migrating has also declined rapidly in a number of partially migratory populations (Sutherland 1998b).

This lability may be explained by the genetic structure of these traits. Migratory behaviour in both birds and insects is hypothesized to follow a threshold quantitative genetics structure (Roff 1986; Pulido *et al.* 1996). The location of the threshold is thought to be environmentally sensitive. Under such a genetic structure the degree of migratory behaviour in the phenotype can change greatly with environmental variation and with relatively mild selection (Pulido 2007). The rapid collapse of migration in ungulates is consistent with a threshold model. However, we know little about the genetic structure of migratory traits in ungulates. In a study of a mixed migratory population of moose (*Alces alces*) in Sweden, Sweanor & Sandegren (1988) found that all 13 calves of 11 migratory cows were migratory as adults and all six calves of four non-migratory females were non-migratory suggesting either a genetic or maternal effect basis for the behaviour. Nelson (1998) in a long-term radio-telemetry study, found that white-tailed deer fawns tend to follow their mother's migratory pattern later in life, although individuals did change from that pattern.

Navigation and orientation mechanisms have been studied in birds and small mammals but not ungulates. In birds there are multiple orientation systems including magnetic, solar and stellar compasses (Wiltschko & Wiltschko 2003). Recent research on small mammals suggests that ungulates and other mammals may be capable of quite complex spatial processing. Studies have documented startlingly literal 2D spatial maps (Hafting *et al.* 2005) as well as place cells (O'Keefe 1976) and head direction cells (Taube *et al.* 1990) in rat hippocampus and associated structures. Intriguingly, multiple maps are present with different scales of resolution (Hafting *et al.* 2005; Frost & Mouritsen 2006).

Much is also known about the physiology of bird migration, including hormone regulation, hyperphagy and fat deposition, and timing of migration with other life events (Berthold *et al.* 2003). These aspects of ungulate migration have received little attention. Particularly interesting is the question of how, in species with temporally variable migration (e.g. Serengeti ungulates), calving is synchronized to the arrival at the calving grounds.

One advantage that ungulates have for studies of migration is that they can support relatively large radio-transmitters. With the advent of GPS tracking and satellite telemetry fine-scale movement behaviour and habitat selection can be carefully examined. This capability allows researchers to address questions related to the responsiveness of migration to environmental change and to assess the spatiotemporal scale over which animals make decisions that drive migratory movements. One possibility is that all movement is merely a sequence of local-scale decisions based on information obtained within the animal's immediate perceptual range. This would suggest that animals follow gradients in a more continuous fashion, making day-by-day or minute-by-minute movement decisions and thus migration is not distinct from local movements. Alternatively, migration could be a consequence of a small number of large-scale decisions that transcend an animal's perceptual range and thus require experience and memory or are genetically encoded, and thus relatively unaffected by local circumstances.

Combining GPS-satellite telemetry with recent analytical advances, ungulate studies have begun to address this question and the results thus far are mixed. Johnson *et al.* (2002) found that the rate of within-patch movements in caribou in British Columbia differ from between-patch movements but found no difference between migratory movements and between-patch movements. This suggests that the decisions caribou make on migration may be no different than the decisions made in their daily between patch movements. On the other hand, in a study of caribou in Quebec, Bergman *et al.* (2000) used telemetry data to parameterize correlated random walk (CRW) models that did distinguish migratory from non-migratory movement. They found that for several months prior to spring calving the CRW models under-predicted displacement because turn directions in this period were negatively autocorrelated in time, indicative of straighter movement than at other times of the year (Bergman *et al.* 2000).

In the Serengeti, the annual migration of wildebeest, zebra and Thomson's gazelle is related to rainfall seasonality and soil type differences that in turn create an annual north-south cycle of variation in food quality, quantity and phenology (Maddock 1979). However, these migrations also show considerable variation between years in timing and route. This variation appears to be related to finer-scale spatial and temporal patterns of rainfall and is well-predicted by new vegetation growth (Boone *et al.* 2006). The Serengeti results suggest that migratory patterns in many ungulates are very flexible and environmentally responsive in terms of route and timing if not endpoints.

Memory or genetics also likely play a role in whether migratory species exhibit seasonal site fidelity. Seasonal site

fidelity is often measured as the percentage of animals returning to a particular site (often having arbitrarily defined boundaries) in a subsequent year (Berry & Eng 1985; Ramsay & Stirling 1990; Lewis *et al.* 1996; Irons 1998; Phillips *et al.* 1998; Flynn *et al.* 1999). Site fidelity is an important concept for the conservation of migratory ungulates for several reasons. First, patterns of breeding site-fidelity are critical in shaping the exchange of genetic information within a population (e.g. Esler 2000; Gill *et al.* 2001). When fidelity is high, each breeding site effectively acts as a separate, isolated population, which can have important implications for its long-term persistence (Lande & Barrowclough 1987) and genetic structure. In birds a change in the non-breeding range of a sub-population can cause assortative mating and genetic differentiation if it changes the arrival date to the breeding grounds and thus increases the likelihood of within sub-population matings (Terrill & Berthold 1990). In ungulate populations that employ several calving grounds, assortative mating can also occur if individuals have high site fidelity and mating occurs on the calving grounds or on migration. In the Tarangire wildebeest population (Box 1), mating and calving co-occur on individual calving grounds, however, the level of site fidelity to these calving grounds is unknown.

Secondly, if habitat disturbance occurs within migratory routes, high fidelity may lead to more rapid population decline as these animals will experience a prolonged period of reduced reproduction and survival in the degraded habitat (Watkinson & Sutherland 1995; Sutherland 1998a). Some migratory bird species display such extreme breeding site fidelity that, despite the removal of all woody vegetation, individuals will still return and search for mates (Wiens *et al.* 1986). In contrast, several other migratory bird species have apparently rapidly expanded their range as a result of the availability of new resources, or possibly, lower competition (Sutherland 1998b). Although migratory ungulates in general display higher site fidelity to breeding than non-breeding sites (Maddock 1979; Dusek *et al.* 1989; Brown 1992; Aycrigg & Porter 1997; Ferguson & Elkie 2004; Sakuragi *et al.* 2004), few studies have quantified the effects of disturbance on patterns of site fidelity (but see: Mahoney & Schaefer 2002).

These questions have important implications for the population consequences of human disruptions of migration. If migration is driven by decision rules implemented at fine-scales, migratory animals should react in a locally adaptive fashion to anthropogenic changes to their migratory pathways. If migration patterns are genetically or culturally encoded, migrations could continue even if they no longer have positive cost-benefit ratios. Additionally, maintenance of portions of migratory routes or dispersal zones to which ungulate populations show high fidelity would clearly be essential to conserving migrations.

Although research on migratory ungulates is more logistically challenging than on birds, we believe that bold and imaginative experiments are possible. A few examples include: delaying individuals until the rest of the herd has left to understand the role of public information, translocating individuals (e.g. Nelson 1994), and studying re-introduced populations. Also, better use can be made of captive or fenced animals to study behaviour, physiology and genetics. There are many challenges that will need to be overcome, not the least of which are animal welfare issues, but the potential payoff in our understanding and ability to conserve migrations is promising.

### Understanding ungulate migrations and preventing their loss

Conservationists have long argued for the importance of protecting migratory routes and dispersal zones of species (Grzimek & Grzimek 1961; Kelsall 1968; Berger 2004; Thirgood *et al.* 2004). However, few protected areas worldwide encompass the entire migratory range for most migratory species, particularly ungulates. For example Yellowstone and Grand Teton National Parks predominantly protect the summer or breeding habitat of elk and pronghorn antelope (*Antilocarpa americana*), while much of the historic winter or non-breeding habitat for these species is found outside of the parks (Berger 2004). On the other hand, national parks in East Africa such as Amboseli, Nairobi, Tarangire (see Box 1), and Lake Manyara conserve primarily non-breeding or dry season habitat for migratory herbivores such as wildebeest, zebra, eland and Thomson's gazelle, with the breeding or wet season habitat for these species occurring almost entirely on adjacent public or private lands (Lamprey 1963, 1964; Western 1975; TCP 1998).

The conservation of migratory ungulates is particularly challenging because unlike birds that have discrete stopover locations along migratory routes, entire regional landscapes must be managed in order to conserve migrations. In addition, migratory routes used by ungulates often vary by season and year, which can further complicate the management of regional landscapes. As human activities increasingly insularize protected areas, migratory routes and dispersal zones are often among the first critical habitats to be lost.

We believe that an integrated research agenda on migratory ungulates is vital to informing the efforts of conservation managers and planners. Research in the following areas would be particularly informative:

- (1) Demographic studies that quantify vital rates during each phase of migration. These will help to understand and predict how habitat changes in each seasonal
- habitat affect population dynamics and seasonal carry-over effects.
- (2) Comparative analyses of similar or co-existing migratory and non-migratory populations to explore the costs and benefits of migration.
- (3) Behavioural and genetic work to characterize the heritability and environmental sensitivity of the traits comprising the ungulate migratory syndrome, and to compare the within and between population variation in these traits.
- (4) Combine movement tracking and modelling with simultaneous physiological and neurobiological measurements to better understand the physiology and behaviour of the migration movements.
- (5) The development of a range of models for particular species that quantitatively synthesize insights from the preceding research foci. Such models should be designed to be useful as decision-support tools for management (Burgman & Possingham 2000).

Many of these research priorities will require advances in our ability to economically mark or recognize many individuals. This may include further advances in telemetry, non-invasive marking methods, and digital pattern recognition for species with distinctive markings.

The great animal migrations that did and still do occur remain perplexing and will require a diverse array of integrated research approaches if we are to conserve them in our changing landscapes. We recognize that even with advances in our understanding of the biology of migration, the practical challenges to conserving migratory populations are great. However, without this understanding even our best conservation efforts may be fundamentally flawed.

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